

HABITAT SUITABILITY INDEX MODEL FOR THE BLACK-FOOTED FERRET: A METHOD TO LOCATE TRANSPLANT SITES

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ABSTRACT.—A Habitat Suitability Index Model (HSI), following the U.S. Fish and Wildlife Service HSI Model Series, is described for the black-footed ferret. The literature on which the model is based is reviewed, and model assumptions and structure are discussed. A realistic model is specified with variables and their functions that embody the critical spatial and resource heterogeneity characteristic of the broad geographic environment ferrets occupy. It assumes that ferrets can meet year-round habitat requirements within prairie dog colonies providing: (1) prairie dog colonies are large enough, (2) burrows are numerous enough, and (3) adequate numbers of prairie dogs and alternate prey are available. Five habitat variables are identified: V1 is the frequency distribution of colony sizes, V2 is the total area of colonies, V3 is burrow opening density, V4 is intercolony distance, and V5 is prairie dog density. Variables are compensatory. As more data become available and our understanding of ferrets expands, the basic model design can readily incorporate improvements without radical restructuring.

Habitat models are an attempt to describe and quantify an animal's essential habitat requirements or "life requisites" and are therefore a useful tool in habitat evaluation. The Habitat Suitability Index (HSI) Model Series, developed by the U.S. Fish and Wildlife Service (USFWS), provides habitat descriptions for several species. These models are useful for assessment of impacts on wildlife and habitat management (USFWS 1980a, b) and may prove especially valuable in endangered species management, where determination of habitat quality and suitability is often critical for management and continuation of the species. HSI "models should be viewed as hypotheses of species-habitat relationships rather than statements of proven cause and effect relationships" (Schamberger et al. 1982:1).

This paper applies the HSI Model format to the Meeteetse, Wyoming environment of the black-footed ferret (*Mustela nigripes*; BFF) as generally described by Clark et al. (*Description and history*, 1986) and more specifically by Forrest et al. (1985)(Fig. 1). Applications and uses of the model are: (1) to compare other areas to BFF habitat at Meeteetse, (2) to use those comparisons to select areas to be searched for BFFs, and (3) to select suitable areas for transplant sites. Our use of the HSI format closely follows the USFWS (1981) and

parallels applications by Allen (1982a, b, 1983, 1984) for other species.

Our use of the HSI model for BFFs incorporates several recent improvements on the roles of ecological models: (1) We stress model reality of a single species more than focus upon model precision or generality (see Levins 1966, Rosen 1978, Kaiser 1979, Pielou 1981). (2) Few highly measurable variables dictate the HSI, and, although some are collinear, together they contain high explanatory power, at the same time allowing comprehensible results and simplified sensitivity analysis. This reflects the growing consensus that there is no apparent relation between model complexity and predictive utility in any field of forecasting (e.g., Ascher 1978, K. E. F. Watt personal communication). (3) Our model uses nonlinear representations of variables, rather than linear, because those more accurately express the dynamic nature of biological responses and realistic species-habitat relations (Whittaker 1975, Green 1979, Westman 1980, Johnson 1981, Meents et al. 1983). Nonlinearity permits us to mimic more realistic biological processes that involve thresholds and limits and the smoothed transitions between them (Holling 1985, J. R. Krebs personal communication). (4) The model variables and their functions embody the critical

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Fig. 1. Photographs of black-footed ferret habitat (prairie dog colonies and prairie dogs) and ferret predation. Photos by Tim Clark.

A. White-tailed prairie dog colony occupied by ferrets.



B. Black-footed ferret at prairie dog burrow.



C. Two white-tailed prairie dogs.



D. Black-footed ferret with prairie dog prey.

importance of spatial and resource heterogeneity. The structural simplicity of the BFF-prairie dog (*Cynomys* spp.) community promotes a design where all variables directly assess spatial patchiness and resource variability, considerations that have pivotal impact on population dynamics and population viability (reviews in Steele 1974, Wiens 1974, Southwood 1977, Shugart 1981).

The outcome of the above four features is only a slight increase in model complexity traded for a dramatic increase in ecological reality. Perhaps of equal benefit is the ease of model validation. As more data become available and our understanding of BFFs expands, the basic model design can readily incorporate improvements without radical restructuring. Data sets already completed and cited below could likely be reevaluated with future model versions.

This HSI application for the BFF draws on Clark et al. (*Description and history*, 1986) and Forrest et al. (1985), who describe the Meeteetse, Wyoming, BFF study area (1981–1985) and its use by BFFs as well as all the data from the Mellette County, South Dakota, BFF study (1964–1974). Because of the localized nature and limited size of these two study areas, this HSI model will likely require updating if BFFs are found in other areas in different ecological settings. In the meantime, this HSI model can serve as a useful tool in BFF recovery planning to evaluate proposed transplant/relocation sites.

BACKGROUND

Requests for evaluation of BFF habitat have been frequently mentioned in the literature. The Black-footed Ferret Recovery Team (1978) requested research to define components of a prairie dog colony necessary to support BFFs. The BFF Recovery Plan also notes the need to establish ideal habitat sites for successful introduction of transplanted BFFs (see Linder et al. 1972). The South Dakota BFF and Prairie Dog Workshop in 1973 suggested several BFF management needs, including a definition of habitat (Hillman and Linder 1973, Stuart 1973, Erickson 1973). Others have discussed the need for BFF preserves and habitat descriptions (Clark 1976, 1984, 1986). Flath and Clark (1986) described historic prairie dog distributions in Montana

for the period 1908–1914. This early Montana situation probably represented a habitat setting in which BFFs evolved among the complex interrelationships of species and environmental interactions of the prairie dog ecosystem.

Hillman et al. (1979) described prairie dog distribution in the area occupied by BFFs in South Dakota. Their description was widely used by management agencies as a guide to the number and spacing of prairie dog colonies to be left after prairie dog eradication programs.

Clark et al. (*Description and history*, 1986) provided a descriptive and historical overview of the Meeteetse BFF environment. Forrest et al. (1985) noted that BFFs are restricted to a prairie dog complex—a group of prairie dog colonies distributed so that individual BFFs can migrate among them commonly and frequently. The 37 colonies of the Meeteetse complex (total size 2995 ha) were described and their occupation history by BFFs noted. The average density of adult BFFs was 1 BFF/56.6 ha. Burrow openings, based on literature reviews, are correlated with the number of prairie dogs present ($r=0.71$). High burrow densities are desirable for BFFs in that they provide added protection from predators and shelter from the elements. Colonies greater than 100 ha supported more than two resident adult BFFs, whereas colonies from 12.5 ha to 102.0 ha supported only one BFF throughout the year. BFFs traveled among the colonies, but to an unknown extent. BFFs may use burrows at low densities and colonies of small size in travels between larger colonies. BFFs moving between colonies have a greater chance of finding another colony if the colonies are large and close together.

Several bibliographies of BFFs (Harvey 1970, Snow 1972, Hillman and Clark 1980, Casey et al. 1986) and of prairie dogs (Clark 1971, in preparation, Hassien 1973) exist. These also serve as background for this HSI model. General information on BFFs is summarized in the bibliographies listed above, in primary sources from South Dakota studies (e.g., Hillman 1968, Henderson et al. 1969, Fortenbery 1972), and, more recently, from Meeteetse, Wyoming (e.g., Clark et al., *Description and history*, 1986; Clark et al., *Descriptive ethology*, 1986; Campbell et al. 1985; Richardson et al. 1985; Forrest et al. 1985; Biggins et al. 1985).

HABITAT USE INFORMATION

Overview

A member of the family Mustelidae, the BFF is the only ferret native to North America (Hall 1981) and is perhaps the rarest and most endangered mammal species on this continent (Cahalane 1954, Hillman and Clark 1980). BFFs are solitary except during breeding and maternal care of young and are primarily nocturnal. They prey on prairie dogs, whose burrows they also use for cover and litter rearing.

Food

The BFF relies on prairie dogs as its primary food source, although other prey, both live and dead, are taken in considerably lesser amounts (Hillman 1968, Henderson et al. 1969, Sheets and Linder 1969, Sheets et al. 1972, Clark et al. 1985). Sheets et al. (1972) found 91% of 82 BFF scats from South Dakota contained prairie dog remains, and Campbell et al. (unpublished data) found 87% of 86 BFF scats from Meeteetse contained prairie dog remains. Prairie dogs, on this basis, compose the major BFF food.

Stromberg et al. (1983) generated a predator-prey model of metabolizable energy requirements that estimated: (1) annual prey requirements for one reproductive female BFF and her litter of four and (2) prairie dog population sizes needed per BFF. Powell et al. (in press) estimated BFF winter energy expenditure (about 104 kcal/day) and prey requirements (about 20 prairie dogs from December through March) at Meeteetse. A lactating female with four young are predicted to need six times the winter estimate, or about one prairie dog per day in summer.

Water

BFFs apparently satisfy water requirements through prey consumption and have never been observed in the wild drinking free water. Henderson et al. (1969) reported that captive BFFs drank water irregularly. L. Richardson (unpublished data) watched a BFF eating snow at Meeteetse.

Cover

Cover for BFFs is provided by prairie dog burrows, which are used for predator avoid-

ance and thermal cover throughout the year (Clark et al. 1985, Richardson et al. in press). Any prairie dog burrow is assumed to be sufficient to satisfy BFF cover requirements. Higher burrow densities provide greater cover.

Reproduction

Reproductive habitat requirements for BFFs are assumed to be identical to food and cover requirements described above because all BFF activities are associated with prairie dog burrow systems (Clark et al. *Descriptive ethology*, 1986; Richardson et al. in press; Forrest et al. 1985). Large, mounded, multi-entranced burrows may be important for litter rearing because of their presumed extensive tunnel network.

Interspersion

A picture of BFF home range patterns is emerging from research efforts at Meeteetse. A single adult male's range may encompass home ranges of several females, which show much smaller ranges (Richardson et al. unpublished data). Females remain with their litters until late summer, when young become independent (Henderson et al. 1969, Clark et al. *Descriptive ethology*, 1986). BFFs appear to have a typical mustelid spacing pattern described by Powell (1979), Forrest et al. (1985), and Richardson et al. (in press). More information is needed on BFF home ranges and movements, dispersal of young or adults, and inter- and intrasexual interactions.

Interspersion characteristics of BFFs represent a two-dimensional management consideration—individual and populational. Individual interspersion patterns are better known than populational interspersion patterns required for minimum population sizes. A resident female snow-tracked from December through March used 16.0 ha and was overlapped by a resident male that used 136.6 ha (Forrest et al. 1985). Studies of radio-collared BFFs show a young female used 12.6 ha in October and November (Biggins et al. 1985). Population interspersion is dependent on the size, configuration, and intercolony distance of prairie dog colonies making up the complex. Data show that, if colonies are too small and intercolony distances are too large, then BFF populations cannot sustain themselves.

The search for food (energetics) becomes prohibitive, avoidance of predators becomes difficult or impossible, and adequate thermal cover is rare or nonexistent, all reducing both individual and population survival.

Special Considerations

Successful management of BFFs depends on maintaining adequate numbers and areas of prairie dog colonies. Minimum viable population (MVP) sizes and area requirements for BFFs were addressed by Groves and Clark (1986). Additional estimates of these variables are underway by Shaffer et al. (in preparation), who are modeling effects of both demographic and environmental stochasticity on BFF populations of varying sizes. The MVP represents a threshold below which populations are not self-sustaining. Populations may persist for a long time below the MVP, but probably at a loss of adaptability and a high susceptibility to local extinction. Groves and Clark (1986) noted that the genetic method of determining MVP for the Meeteetse BFFs estimated that about 200 animals are needed for maintenance of short-term fitness. The estimated 200 animals needed is about four times the number of breeding adults estimated to currently exist at Meeteetse (Clark 1986).

Poisoning and shooting of prairie dogs should be prohibited from areas where BFFs occur as well as from other selected portions of prairie dog range. Hubbard and Schmitt (1984) suggested a "refugia" concept of managing prairie dogs in which relatively large areas are omitted from poisoning and other disturbance. They suggested that refugia be large enough to support a BFF MVP and based such area estimates on the Stromberg et al. (1983) predator-prey model. Clark (1986) outlined a series of management guidelines for BFFs.

Differences in black-tailed (*C. ludovicianus*) and white-tailed prairie dog colonies have been noted (Tileston and Lechleitner 1966, Campbell and Clark 1981, Clark et al. 1982). Black-tailed colonies often show greater prairie dog and burrow opening densities—two important variables of BFF habitat. Satisfying habitat requirements for BFFs on white-tailed colonies as described in our HSI model is assumed also to satisfy habitat re-

quirements on black-tailed and Gunnison's (*C. gunnisoni*) prairie dog colonies.

APPLICATION OF HABITAT SUITABILITY MODEL

Model Applicability

Geographic area.—Although this model was developed on data from the only two BFF populations ever studied, it should apply throughout the historic range of the BFF until additional BFF populations in different ecological settings are found, studied, and results show it does not apply. Even though a single prairie dog colony cannot support a BFF MVP (unless it is extremely large), it can potentially support one or more individuals. Therefore, any prairie dog colony should be considered potential BFF habitat. Historic and current land use patterns affect the quality of BFF habitat. A constellation of prairie dog colonies, described by Clark et al. (*Description and history*, 1986) and Forrest et al. (1985) as a prairie dog "complex," is needed to support a BFF MVP.

Season.—This model has been developed to compare year-round BFF habitat at Meeteetse to habitat in other areas. Because prairie dogs may become torpid or hibernate over winter at northern latitudes, it is recommended that evaluation take place when prairie dogs are active and when snow cover is minimal or absent: late May to late June is recommended.

Cover Types.—This model compares the BFF habitat at Meeteetse to other potential BFF habitat in all cover types where prairie dogs are found.

Minimum Habitat Area.—Minimum habitat area, as discussed for BFFs by Forrest et al. (1985), is defined as the amount of contiguous habitat that is required before an area will be occupied by a species (Allen 1982a). We recommend that a preliminary estimate of 4,000–6,000 ha of prairie dogs is needed to support a MVP of 100 BFFs (Forrest et al. 1985, Groves and Clark 1986).

Model Review.—Drafts of this model were reviewed by our colleagues in the Idaho State University/Biota Research and Consulting, Inc. ferret study team—Steven Forrest, Louise Richardson, Tom Campbell, and Denise Casey; Arthur Allen, Habitat Evaluation Procedures Group, USFWS; Wayne Brewster and Ronald Crete, Office of Endangered Spe-

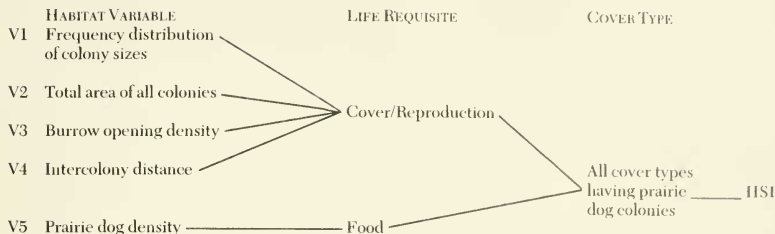


Fig. 2. The relationship of habitat variables, life requisites, and cover types to the HSI for the black-footed ferret.

cies, USFWS; Donald Streubel, Department of Biological Sciences, Idaho State University; Craig Groves, Idaho Heritage Program, The Nature Conservancy; Mark Stromberg, The National Audubon Society; John Hubbard, Endangered Species Program, New Mexico Game and Fish; John Cada and Dennis Flath, Nongame Program, Montana Department of Fish, Wildlife, and Parks; Harry Harju, Wyoming Game and Fish Department; and Sid England and Dale Lott, Department of Wildlife and Fisheries Biology, University of California-Davis. Improvements and modifications suggested by these persons are appreciated and were incorporated into this model.

Model Description

Overview.—The BFF can meet its year-round habitat requirements within prairie dog colonies providing: (1) prairie dog colonies are large enough, (2) burrows are numerous enough, and (3) adequate numbers of prairie dogs and alternate prey are available. This model therefore assumes that reproducing populations of BFFs use only prairie dog colonies, and habitat evaluation based on this model considers only the life requisites provided by such colonies. BFFs do not rely solely on prairie dogs for food, but breeding populations may depend on prairie dog colonies with their host of associated vertebrates, many of which are known food items. It assumes that these colonies will provide a sufficient prey base (including alternative prey) and sufficient burrow openings for predator evasion and as sites of litter rearing, thus providing maximum potential for BFF habitat. Ecological differences in habitat

may be found if future populations of BFFs are discovered, or if BFFs are found on areas other than prairie dog colonies.

The following section documents the logic and assumptions used to translate habitat information for the BFF to the variables and equations used in the HSI model. Specifically, this section covers: (1) identification of variables used in the model, (2) definition and justification of the suitability levels of each variable, and (3) description of the assumed relationship between variables. The BFF habitat variables have been grouped into two sets: (1) an aggregated set of four variables that assess cover/reproduction as life requisites and (2) a single life requisite variable for food. Figure 2 illustrates the relationship of habitat variables, life requisites, and cover type for the BFF. The five habitat variables identified under the two life requisite categories are: V1 is the frequency distribution of colony sizes, V2 is the total area of colonies, V3 is burrow opening density: average number of burrow openings per ha of colony, V4 is intercolony distance: mean distance between colonies (these four variables are grouped under the cover/reproduction life requisite), and V5 is prairie dog density: mean number of prairie dogs per ha (this variable is the food life requisite). The aggregated variables are viewed as compensatory (i.e., an increase in one variable will increase the HSI, but not the suitability of other variables) and thus are combined to produce a single HSI. The limiting factor method is suggested for evaluating resulting values of the two variable sets.

Cover/reproductive component.—BFFs rely on prairie dog burrows for cover and litter rearing. Four variables are defined.

Variable 1 examines the relationship between the distribution of prairie dog colony sizes in a region and its Suitability Index. Prairie dog colonies present at the turn of the century represented extremely large areas of contiguous prairie dog distribution (e.g., in Montana see Flath and Clark 1986). Such areas represented a 100% prairie dog occupancy and were assumed to be optimal habitat for BFFs. By comparison more recently, Mellette County, South Dakota, showed 1.7% of its area occupied by prairie dogs, with a mean colony size of about 9 ha (Hillman et al. 1979). The Big Horn Basin of Wyoming containing the Meeteetse BFFs has about 1.7% of its area occupied by prairie dogs in many small, low-density colonies, although a few exceed 1,000 ha (Clark et al. *Description and history*, 1986). Clark et al. (1982) described several sample areas in New Mexico that showed about 1% in prairie dogs, with colony sizes averaging 33 ha (range 10–61 ha); in Utah about 1.9%, with colony sizes averaging 33 ha (range 2–73 ha); in Wyoming on Thunder Basin National Grassland about 1.3% in prairie dogs showing a wide range in colony sizes; in southern Wyoming about 3.2% in prairie dogs, with colony sizes ranging up to 2,500 ha; and in another area in Utah, colonies averaged 125 ha (range 0.2–958 ha). The total sizes of these areas varied, and this fact clearly influenced the distribution of prairie dog colony size located. If a line is drawn around the prairie dog complex at Meeteetse (least polygon enclosing all 50+ ha colonies) and the area occupied by prairie dogs inside this polygon is calculated (about 130 sq km), then about 22% of the area is occupied by prairie dogs. The 50 ha figure does not mean that smaller colonies are not important to BFFs; indeed the smaller colonies are used at Meeteetse (Forrest et al. 1985). Colony size distribution within this area is listed in the Appendix (Table 3).

VI is a multidimensional probability estimate and is not graphable as are the remaining variables. The Appendix describes computation of VI.

Variable 2 is the total area of prairie dog colonies. Assuming a BFF MVP consists of 100 breeding adults (even though Groves and Clark [1986], using genetic methods, estimated 200),

then 100 colonies of 50 ha each (about 5,000 ha) is required to support them. It is assumed that greater colony area means greater sites for cover and reproduction for BFFs.

Variable 3 is burrow opening density: the average number of burrow openings per ha of colony. Colonies at Meeteetse are characterized by burrow opening densities as low as 10 openings/ha and up to 100+ openings/ha. This compares with other areas ranging 21–135/ha for black-tails, 32–57/ha for Gunnisons, and 2–64/ha for other white-tails (Clark et al. 1982). It is assumed that the greater the burrow opening density, the greater the cover and sites for successful rearing of young.

Variable 4 is the mean of intercolony (nearest neighbor) distances. This variable is essential for cover/reproductive requirements but is also essential for expansion of BFF populations and dispersal. In pristine times, BFFs in large colonies may have dispersed from their natal areas to new areas without ever leaving the single large prairie dog colony. Dispersal between colonies, where escape cover is minimal or absent, is thought to expose BFFs to high rates of mortality. Intercolony distance at Meeteetse is about 0.92 km (range 0.13 to 3.70). In South Dakota intercolony distance averaged 2.4 km. Intercolony distance for a sample of 11 Gunnison's colonies in New Mexico, Colorado, and Utah was 2.4 km and for 33 white-tailed colonies in Utah and Colorado was 4.9 km. In winter at Meeteetse BFFs in intracolony movements often travel 2+ km per night hunting. Movements up to 8 km have been noted during the breeding season. It is assumed that the smaller the intercolony distance, the higher the quality of BFF habitat.

Food component.—Food is described by a single variable.

Variable 5 is prairie dog density (number/ha). High densities of prairie dogs provide increased opportunity for BFFs to successfully meet their energy and nutrient requirements as well as providing alternate prey associated in prairie dog colonies. Additionally, a high density of prairie dogs means an increased density of burrows, which is related to the previous variables as well.

TABLE 1. Equations for determining year-round life requisites for the black-footed ferret (2.0 is included as a scaling factor).

| Life requisites | Cover type | Equation |
|--------------------|--|---|
| Cover/Reproduction | All cover types where prairie dog colonies occur | $(2 \times V1 \times V2 \times V3 \times V4)^{1/4}$ |
| Food | Same as above | V5 |

Variable Relationships

Suitability of BFF habitat depends entirely on attributes of prairie dog colonies. V1 converts the distribution of colony sizes (relative to the total colony area) into a single SI measure. V2 accounts for the total area of colonies relative to BFF requirements and is especially discriminative in the range of MVP area size. V3 gauges the value of colonies in terms of cover (burrow opening density) and, although it generally covaries with food (V5: prairie dog density), any particular case may be critically uncorrelated. V4 (intercolony distance) appraises the effect of colony dispersion in reference to BFF mobility and behavior. In summary, V1 reflects colony size distribution, V2 the total colony area the size distribution represents, V3 the cover value of the colonies, V4 the spatial dispersion of those colonies, and V5 the food value of the colonies.

Suitability Index (SI) graphs and equations for habitat variables.—This section contains suitability index graphs and equations that illustrate the habitat relationships described in the previous section (Fig. 2).

Equations.—Life requisite values for the BFF can be obtained by combining the SI values through the use of equations (USFWS 1981). A description and explanation of the assumed relationship between variables was included under the Model Description, and the specific equations in this model were chosen to mimic those perceived biological relationships as closely as possible. The suggested equation for obtaining year-round life requisite values for the BFF are given in Table 1. The four cover/reproduction variables are multiplied by two (a scaling factor for V1) and aggregated by using the geometric mean, GM. We necessarily use the GM because the quantities involved are measured on a ratio scale and the variables are not arithmetic sequences but geometric.

VARIABLE

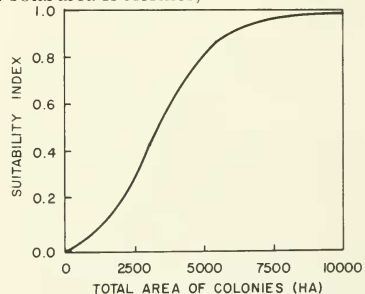
V1 Distribution of colony sizes,

$$P(AB|N_i, i) = \frac{\sum_{i=2}^k N_i \binom{k}{i}}{\left(\sum_{i=1}^k N_i \times i \right)^2}$$

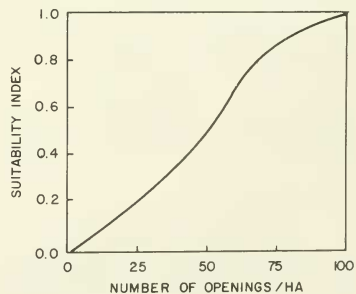
With n_i as the number of colonies of size i , the resulting probability increases nonlinearly with increase in colony sizes (numerator) relative to the size of the complex (denominator) (see Appendix for example calculations of this equation)

VARIABLE:

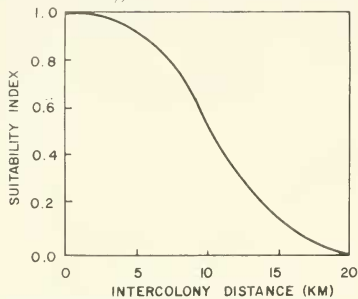
V2 Total area of colonies,



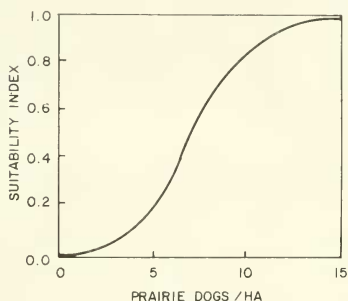
V3 Burrow opening density (mean number of burrow openings/ha of colony),



V4 Intercolony distance (mean distance between colonies),



V5 Prairie dog density (mean number of prairie dogs/ha of colony),



HSI determination.—The HSI for the BFF will equal the lowest of the SI values obtained for either the Cover/Reproduction or Food life requisite. This recognizes limiting factors. The fact that V2 only scales to 10,000 ha of total colony area reflects the importance of an MVP area and does not mean that even greater-sized prairie dog complexes are not more desirable. The larger the complex the better. The largest complex sizes available should be selected for BFF translocations, and these should exceed the size of Meeteetse (Appendix). An HSI approaching 1.0 is ideal and not necessarily attainable; that is, a mathematical ideal or extreme to compare against—in actuality, perfect habitat does not exist.

Application of the Model

Definitions of variables and suggested field measurement techniques are presented in

Table 2. Vegetative cover types for each variable are those that contain prairie dog colonies. The Appendix contains HSI calculations for Meeteetse and two other areas. These are presented as examples of model application, for ease of application of HSI to other areas, and for comparative purposes.

Interrelationships

Three considerations from application of the HSI format to the Meeteetse BFF environment as described in the Appendix must be addressed. First, the Meeteetse HSI of 0.590 for the cover/reproductive variables is midrange in a HSI range of 0–1. Prairie dog complexes should be located that exceed the Meeteetse HSI and that can support large BFF populations well above the MVP. It is the low V2 (complex size or total colony area) that deflates the overall HSI. Second, if high HSI areas cannot be located that can support a MVP, then a series of smaller areas showing a lower HSI than Meeteetse will have to be utilized in a complex, complementary, and closely managed situation. Third, application of the HSI format to the prairie dog area in Mellette, South Dakota, may show that its HSI is well below estimated MVP requirements. If so, this means that management for a minimum area and colony size pattern as suggested by Hillman et al. (1979) has been below the area needed to sustain a MVP of BFFs and that new recommendations are needed.

SOURCES OF OTHER MODELS

No habitat models for the BFF were located in the literature except for descriptions of BFF habitat by Hillman et al. (1979), Stromberg et al. (1983), and Forrest et al. (1985).

CONCLUDING REMARKS

If the prairie dog colony size distributions shown in Table 3 of the Appendix are typical of prairie dog complexes, then in terms of prairie dog complex area, the sum influence of most colonies will be less than the few very large ones. Distributions with this property of aggregation or clumping are called contagious and can often be modeled by generalized discrete distributions (reviews in Coleman 1964,

TABLE 2. Definitions of variables and suggested field measurement techniques.

| Variable definition | Suggested technique |
|---|--|
| V1 Frequency distribution of colony sizes (all inhabited by prairie dogs) | Accurately map colony configurations, determine colony areas from maps; ground surveys are best, but some preliminary aerial surveys may be needed first |
| V2 Total area of colonies (all inhabited by prairie dogs) | Total area of all colonies in the study area based on accurate mapping determined for V1 |
| V3 Burrow opening density (number/ha of colony) | Walk colonies and count holes, or sample selected areas |
| V4 Intercolony distance (mean distance between colonies) | Measured from the edge of a mapped colony along the shortest distance to the next nearest colony |
| V5 Prairie dog density (mean number of prairie dogs/ha of colony) | Use minimal visual counts of prairie dogs active .5–2 hrs after sunrise on three consecutive mornings in mid-June; live capture-mark/recapture population estimate in mid-June |

Douglas 1979). If we view the colonies in a prairie dog complex distributed as a Poisson variate and assume the number of ha per colony has a highly nonrandom logarithmic distribution, then we may obtain the Poisson-logarithmic compound distribution (a type of negative binomial). However, the colony size distributions could not be fit to this distribution even when larger colonies were ignored. This illustrates the extreme "contagion" of prairie dog aggregation and, consequently, the disproportionate effect of such large clusters on the outcome of any realistic model concerning BFF MVPs.

In conclusion, from a statistical standpoint, the most effective and, therefore, most intensive and accurate data collection could be concentrated in the large colonies (in fact, as a nonlinear function of size) with little loss of accuracy. In other words, the model is very robust to small colony exclusion. Indeed, for all variables except V4, which equally weights colony location and therefore dispersion effect, small colonies could be ignored for data collection in MVP-sized complexes when considering cost and time budgeting.

ACKNOWLEDGMENTS

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APPENDIX

Calculations of HSI for Meetetse and two Other Areas

Variable values are most often arrived at by sampling techniques which produce confidence limits. In addition, stratified sampling or consideration of subsets of an area may produce a large range of possible variable values for calculation. For ease of computations

and sensitivity analysis, the equations for VI-V5 are given below and are easily computed on handheld calculators.

Structure of VI

Colony size has been stressed in terms of successful reproduction and energetics. VI appraises this important aspect of colonies by producing higher values for size distributions containing larger colonies and disproportionately lower values for a distribution (given the same area) containing smaller colonies. The following analogy may improve our understanding of this. Assume we have two BFFs, A and B, and wished to distribute them on their own one-hectare plot in a number of Total Areas, each of which contains a different number of colonies totaling a constant area. We drop the two BFFs randomly over these areas and note where they fall. In areas containing a few large colonies, BFFs A and B are noted to land more often on the same colony; in areas of many small colonies, A and B rarely share the same colony. Formally, if we divided a sample space (Total Area) into n subspaces (colonies) where 1 to k are colonies of size i and N_i is the number of colonies of size i , then the probability of any two objects (BFFs A and B) co-occurring in the same subspace (colony) is

$$P(AB|N_i, i) = \frac{\sum_{i=2}^k N_i \binom{i}{2}}{\binom{\sum_{i=1}^k N_i \times i}{2}}$$

$$\text{Since } \binom{x}{2} = \frac{x!}{2!(x-2)!} = \frac{x^2 - x}{2}, \text{ then}$$

$$P(AB|N_i, i) = \frac{\sum_{i=2}^k N_i (i^2 - i)}{\left(\sum_{i=1}^k N_i \times i \right)^2 - \sum_{i=1}^k N_i \times i}$$

In reduced form, solving for $P(AB|N_i, i)$ is simply combining two summations. Summate $N_i (i^2 - i)$ and store in memory M_1 . At the same time summate $N_i \times i$ and store in memory M_2 , then calculate

$$\frac{M_1}{M_2^2 - M_2}$$

TABLE 3. Colony sizes for Meeteetse (Area I), another prairie dog complex (Area II), and a hypothetical complex (Area III). The frequency distribution is in order of colony size and grouped in three size class frequencies.

| Colony numbers | Colony sizes in hectares | | |
|----------------|--------------------------|---------|----------|
| | Area I | Area II | Area III |
| 1 | .5 | | |
| 2 | .5 | | |
| 3 | .5 | | |
| 4 | 1.0 | | |
| 5 | 1.5 | | |
| 6 | 2.0 | | |
| 7 | 2.5 | 3 | |
| 8 | 2.5 | 4 | |
| 9 | 3.0 | 5 | |
| 10 | 3.5 | 6 | |
| 11 | 5.0 | 7 | |
| 12 | 6.0 | 8 | |
| 13 | 8.5 | 10 | |
| 14 | 9.0 | 11 | |
| 15 | 9.5 | 12 | |
| 16 | 11.0 | 14 | |
| 17 | 12.5 | 15 | |
| 18 | 20.5 | 19 | |
| 19 | 21.0 | 20 | |
| 20 | 24.0 | 21 | |
| 21 | 24.5 | 22 | |
| 22 | 26.5 | | |
| 23 | 30.5 | | |
| 24 | 31.5 | 31 | |
| 25 | 31.5 | 34 | |
| 26 | 49.5 | 49 | |
| 27 | 50.5 | 67 | |
| 28 | 51.5 | 81 | |
| 29 | 69.5 | 87 | |
| 30 | 97.5 | 143 | |
| 31 | 102.0 | 151 | |
| 32 | 153.0 | 231 | |
| 33 | 183.0 | 257 | |
| 34 | 196.5 | 617 | 200 |
| 35 | 211.0 | 658 | 2100 |
| 36 | 230.0 | 671 | 2200 |
| 37 | 1307.0 | 2242 | 2300 |
| Total area | 2990 | 5496 | 6800 |
| Total colonies | 37 | 29 | 4 |

All colonies <1 ha are entered as 1 ha. Since colony sizes are often unique numbers or are entered that way as data, then N_i is completely eliminated from the calculations (see example). However, if each colony area is not estimated for some reason, then they can be grouped into intervals such as 0-5 ha, 5-10 ha, etc., in which case the midpoint can be used (i.e., 2.5, 7.5).

Structure of V2-V5

Variables 2, 3, 4, and 5 are intrinsically non-linear and are each derived from the differential equation $dy/dt = ay^2 + by + c$ and simplified to the logistic form of

$$Y = (1 + ke^{-rt})^{-1}$$

The logistic form is particularly suitable in describing these variables because it depicts two asymptotic limits (at 0 and 1 adjustable toward infinity) and contains an inflection point around which the most rapid rate changes occur. For example, intercolony distance (V4) reflects the ability of BFFs to intercept life requisites upon leaving one colony for another. If a straight-line 10 km is as much as BFFs might move in a night, then that value is the inflection point around which critical and therefore extreme shifts in the suitability index (SI) occur. Of course, BFFs easily move from 0 to 5 km and SI values change little within that range. Likewise, once a BFF is well past the "point-of-no-return," say 15-20 km, SI value shifts are also small. Another view is that the chance of intercepting another colony along a radius extending from its home colony is a quadratic function of distance moved modified by the actual mobility and energetic characteristics of the BFF.

$$\begin{aligned} \text{V2: } f(x) &= (1 + 20 e^{-.0009x})^{-1} && \text{x ha} \\ \text{V3: } f(x) &= (1 + 15 e^{-.003x})^{-1} && \text{x burrows/ha} \\ \text{V4: } f(x) &= 1 - (1 + 70 e^{-.4x})^{-1} && \text{x km} \\ \text{V5: } f(x) &= (1 + 200 e^{-.38x})^{-1} && \text{x prairie dogs/ha} \end{aligned}$$

Examples of HSI Calculations

Table 3 contains colony sizes for the Meeteetse complex (Area I), an actual prairie dog complex elsewhere (Area II), and a hypothetical area (Area III). Maps of these three areas follow (Fig. 3). Before computing VI with this data, it is important to understand that although Area I and Area II have different distributions of absolute colony size, the distributions are quite similar in colony size relative to their total colony area. It is V2 that will account for the almost double total area of Area II.

VI: First, calculate

$$\sum_{i=2}^k N_i (i^2 - i).$$

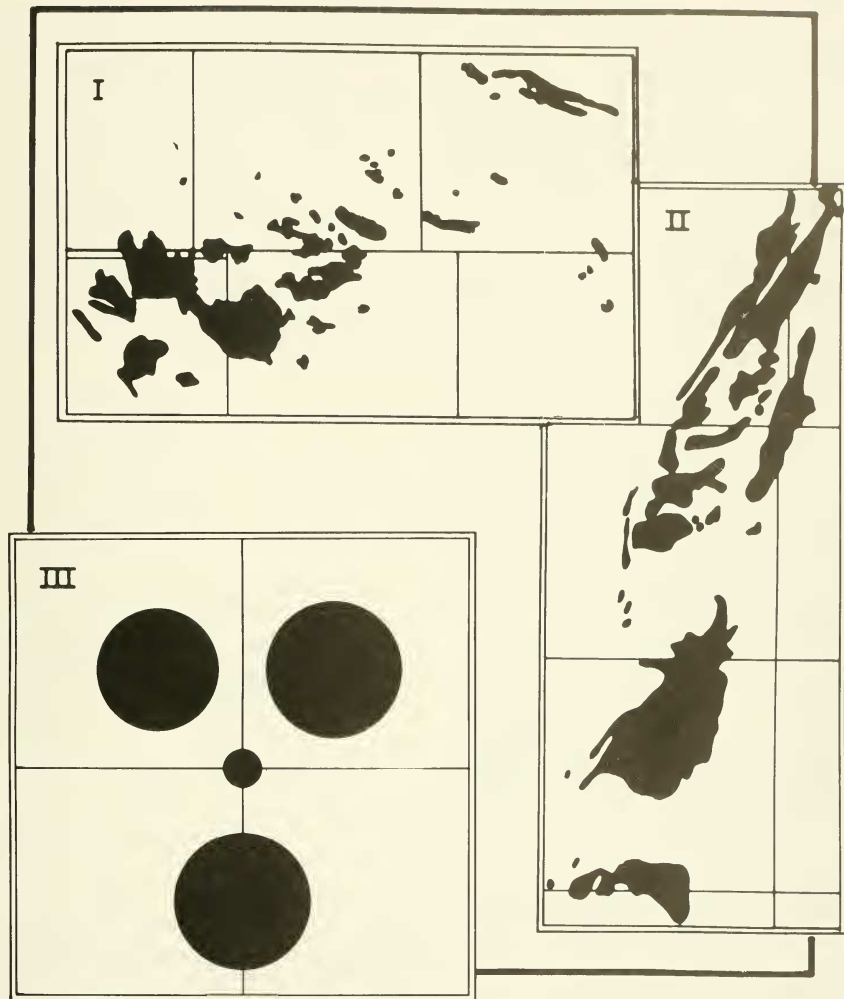


Fig. 3. Maps of prairie dogs complexes used in examples of calculations of HSI. Area I = Meeteetse, Wyoming, Area II = another actual complex, Area III = hypothetical complex.

Since each colony has a different area, N drops out and we add the following series for Table 3 showing colony sizes for each area:

$$\text{Area I: } (1.5^2 - 1.5) + (2^2 - 2) + \dots + (230^2 - 230) + (1307^2 - 1307) = 1,936,862$$

$$\text{Area II: } (3^2 - 3) + (4^2 - 4) + \dots + (671^2 - 671) + (2242^2 - 2242) = 6,473,430$$

$$\text{Area III: } (200^2 - 200) + (2100^2 - 2100) + (2200^2 - 2200) + (2300^2 - 2300) = 14,573,200$$

Note that we do not include areas of size 1; $1^2 - 1 = 0$.

Second, calculate

which is really only the total colony area manipulated as in the first calculation:

$$\left(\sum_{i=1}^K N_i \times i \right)^2 - \sum_{i=1}^K N_i \times i,$$

Area I: $2990^2 - 2990 = 8,937,110$
 Area II: $5496^2 - 5496 = 30,200,520$
 Area III: $6800^2 - 6800 = 46,233,200$

We arrive at V1 by dividing the first by the second calculations for each area: $V1 = P(AB) = .217$ for Area I, $.214$ for Area II, and $.315$ for Area III.

Notice the influence of Area I and II's largest colony on the outcome of the first calculation. Area I: $1307^2 - 1307 = 1,706,942$ and for Area II: $2242^2 - 2242 = 5,024,322$. If we were to split Area I's 1307 ha colony into two separate colonies, it would decrease the value of V1 to $.131$. How far apart these colonies would be is accounted for by a simultaneous increase or decrease of V4. For instance, note how the small 200 ha colony in Area III is a stepping stone between the three larger colonies. Its critical position is reflected by a lower mean intercolony distance and therefore a higher value for V4.

Graphs of the variable equations and the above values follow.

Completing the other values we obtain:

| Variable | Area I | Area II | Area III |
|-----------------|-------------|-------------|-------------|
| V1 | .217 | .214 | .315 |
| V2 (ha) | .424 (2990) | .876 (5496) | .958 (6800) |
| V3 (burrows/ha) | .671 (57) | .385 (37.3) | .992 (125) |
| V4 (km) | .980 (.92) | .980 (1) | .969 (2) |
| HSI = | .590 | .613 | .873 |
| V5 (dogs/ha) | .214 (5) | .155 (4.5) | .987 (12) |

HSI for:

Area I = $(2 \times .217 \times .424 \times .671 \times .980)^{1/4} = .590$

Area II = $(2 \times .214 \times .876 \times .385 \times .980)^{1/4} = .613$

Area III = $(2 \times .315 \times .958 \times .992 \times .969)^{1/4} = .873$

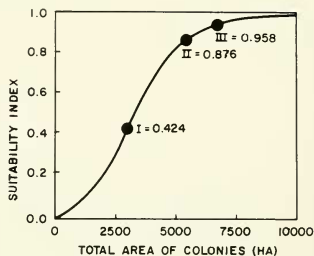
VARIABLE

V1 Distribution of colony sizes

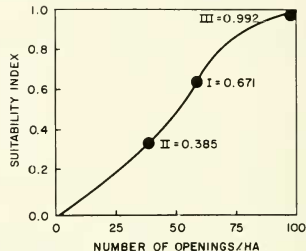
$$P(AB|N, i) = \frac{\sum_{i=2}^k N_i \binom{i}{2}}{\binom{\sum_{i=1}^k N_i \times i}{2}}$$

Using the above equation for V1, area I = $.217$, Area II = $.214$, and Area III = $.315$.

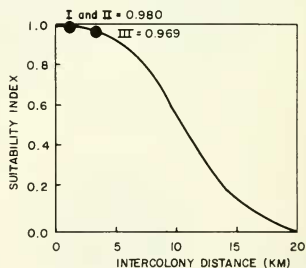
V2 Total area of colonies



V3 Burrow opening density (mean number of burrow openings/ ha of colony)



V4 Intercolony distance (mean distance between colonies)



V5 Prairie dog density (mean number of prairie dogs/ha of colony)

